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**THE ORIGIN AND EVOLUTION  
OF THE DINOSAUR INFRAORDER CARNOSAURIA\***

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Based on a revision of the systematic composition of the carnosaur families, a new diagram of the phylogenetic relationships within the infraorder is proposed. The question of carnosaurs cannot be considered to be resolved.

Excluding the Triassic forms, carnosaurs in the broad or narrow sense have always been considered to be a group of theropods because they are only slightly different from them in fundamental features associated with large body size and a predatory lifestyle. The Late Triassic genera, such as *Teratosaurus* and *Sinosaurus* [33], were assigned to these on the basis of extremely meager material and without sufficient justification. This assignment has subsequently been rejected by most authors [13, 16, 17, 24, 25]. Huene [23] suggested that, along with the Sauropoda and Prosauropoda, the carnosaurs form a natural group Pachypodosauria, within which they are thought to be direct descendants of the prosauropods (the carnosaurs proceed directly from *Teratosaurus* through *Magnosaurus*). Studies of abundant cranial material (which actually belongs to *Sellosaurus gracilis* Huene) gave reason to think that the first species had been a prosauropod, whereas typical material (maxilla, ischium) belong to thecodonts from the family Poposauridae [24].

Huene's diagram, which initially did not receive support, was widely propagated by the discovery of an unusual carnosaur *Torvosaurus tanneri* Galton et Jensen in the Upper Triassic deposits of Colorado [25]. The exceptionally plesiomorphic nature of some of its features, in the authors' opinion, gave sufficient justification for removing them from the prosauropods. What is more, this discovery compelled them to turn their attention to the prosauropod features found in other carnosaurs.

Colbert [16], who isolated the dolichoiliac and brachyiliac pelvic structures in saurischians, used this as a basis to combine the prosauropods and Triassic "carnosaurs" into the suborder Palaeopoda, thereby removing them from the true post-Triassic carnosaurs and to some degree anticipating the discovery of forms that were similar to *Torvosaurus* but had an intermediate type of pelvic structure. By itself this separation was extremely justified, although the initial carnosaur and some palaeopods retain their similarity in a number of essential features: unique tendencies for adapting to predation and bipedalism; reduction of the forelimbs, which with high probability indicates the commonality of the group origins. Nevertheless, the predatory palaeopods (*Teratosauria* [17] or *Herrerasauria* [26]) and carnosaurs diverged significantly. This divergence was expressed, in part, by the formation of brachyilia and dolichoilia, and the first was apparently a

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derivative of the second [16, 36]. The features noted in both cases indicate that the carnosaurs have a monophyletic origin, which is supported by other synapomorphic features: the presence of preorbital fenestrae, the absence of a diastema between the premaxilla and maxilla, intense distal widening of the pubis, the large ascending process of the astragalus, the loss of the exterior digits from the hand, the mesotarsal talocrural articulation, the difference in the structure of the anterior movable and posterior immovable parts of the tail, etc. Not all of these features attest to the “prosauropod” hypothesis, such as, for example, the pelvic structure. For this reason, using Huene’s hypothesis on a new foundation the *Torvosaurus* morphology, in which the features of carnosaur and prosauropods are very uniquely biased, precludes other equivalent hypotheses, sometimes even suggesting that torvosaurus be excluded from the carnosaurs. Moreover, the lack of *Torvosaurus* material, namely the almost total lack of skull material prohibits speaking more categorically in favor of the prosauropod hypothesis of carnosaur origins.

Even the example of the unique hypothesis on origins presented shows that understanding the evolution of large theropods is fraught with many difficulties. First, the majority of carnosaurs have been found in Campanian-Maastrichtian deposits, whereas they are quite rare in Jurassic and Lower Cretaceous deposits. Beyond the Late Cretaceous Tyrannosauridae, only five more ancient forms have been described in detail: *Allosaurus*, *Szechuanosaurus*, *Yangchuanosaurus*, *Piatnitzkysaurus*, and *Eustreptospondylus*—the phylogenetic value of which is drastically reduced by affiliation in its young species.

Second, the taxa have been established on one or, in the best of circumstances, two or three more or less complete skeletons, and most often on fragmentary material.

Third, these taxa have been established on the basis of their differences from other known taxa. However, that a taxon is somewhat different does not mean that it can be adequately classified: these different taxon roles cannot always be established from the preservation factor. The difference may be established on one or two characteristic features, whereas the development of an adequate classification scheme depends on the maximum possible number of characteristic features and, as with the carnosaurs, often from a greater number than are known at the present time.

The family level classification scheme that has been adopted according to present knowledge was constructed for genera that were represented by more complete material. In spite of this, the assignment of some genera to certain families has a formal nature because it is based on features that do not always belong to the entire family as a whole:

**Family Megalosauridae**

*Gasosaurus*, *Iliosuchus*, *Magnosaurus*, *Megalosaurus*, *Metriacanthosaurus*, *Sarcosaurus*, *Yangchuanosaurus*, *Piveteausaurus*.

**Family Torvosauridae**

*Erectopus*, *Torvosaurus*, *Poekilopleuron*

**Family Spinosauridae**

*Spinosaurus*, *Altispinax* (?)

**Family Streptospondylidae**

*Eustreptospondylus*, *Streptospondylus*

**Family Abelisauridae**

*Abelisaurus, Carnotaurus, Xenotarsosaurus*

**Family Allosauridae**

*Acrocanthosaurus, Allosaurus, Chilantaisaurus, Marshosaurus, Piatnitzkysaurus, Szechuanosaurus, Ornithomimoides, Comptosuchus*

**Family Tyrannosauridae**

*Albertosaurus, Alectrosaurus, Alioramus, Daspletosaurus, Tarbosaurus, Tyrannosaurus*

Another hypothesis [16] is still significant. According to this hypothesis, the carnosaurs and late coelurosaurs descended from Triassic coelurosaurs which at present may quite feasibly be grouped in the family Podokesauridae. Using the generalized appearance of bipedal predators, other investigators [4, 45] have included the Triassic coelurosaurs among the ancestors of carnosaurs. This hypothesis was presented in a somewhat altered form (considering them to be sister groups) by Bonaparte [7], Gauthier [26], and Thulborn [53].

Proponents of this view agree that segregating the carnosaurs from the theropods and especially the coelurosaurs that are most similar to them must have occurred at or before the end of the Triassic. By this time the coelurosaurs were already fairly isolated and had established fundamental paths of adaptive evolution. True carnosaurs were unknown before the start of the Jurassic and the specialization of their very earliest Late Triassic branches indicates a fundamentally different, perhaps in Triassic coelurosaurs, direction of evolution. Although in a number of features (formation of the dolichoiliac pelvis, reduction of the outside pedal digits, the foot assuming an overall avian appearance, and reduction of the outside manual digits) they continued to develop in parallel up the end of the Mesozoic. This makes it impossible to rule out the possibility that carnosaurs and coelurosaurs diverged into the earliest stages of saurischian evolution, which is supported by certain features of the skull, pelvis, and forelimbs. This leads us to think that carnosaurs originated independently from thecodonts of the lagosuchid, poposaurid, or ornithosuchid type.

Walker [55, 56] expressed just such an opinion and it was subsequently adopted by other authors [5, 15, 18, 28, 43]. Walker's proposal did not initially attract widespread support because of conflicts associated with the structure of the talocrural articulation: structurally speaking, the tarsals of the Ornithosuchidae are similar to those of crocodiles (in truth, they have a rotating tarsal) and are quite different from those of dinosaurs. It was commonly assumed that the crocodilian and dinosaurian articulations are apomorphic and neither could be a derivative of the other [6, 37, 56]. Charig's work [12] has all but eliminated this obstacle and, following the discovery of an intermediate articulation structure in *Lagosuchus* that is somewhere between the normal crocodilian and dinosaurian intertarsals [7], any doubts about the possibility that the first type of articulation could have transformed into the second have disappeared entirely [18, 52, 55]. In spite of this, not every thecodont family could have been a carnosaur ancestor. It has been shown that the structure and function of the hind limb, especially in the hip joint, are quite different in theropods and Rauisuchidae, which renders the notion of any direct genetic ancestor-descendant relationships in them impossible.

The similarity of the Ornithosuchidae, or Lagosuchidae and to a lesser degree the Rauisuchidae, on one hand and carnosaurs on the other that is possibly associated with a predatory lifestyle and sometimes with bipedalism is striking. As we see it, carnosaur ancestors may be sought among the first three thecodont groups, although we prefer to think of them as being closer to their ancestors by considering one of these families to be a sister family as was done, for

example, with the Ornithosuchidae [43]. The fact that all of the enumerated families include the plantigrade forms, in contrast to the digitigrade dinosaurs, supports this approach. This suggests that carnosaurs and their thecodont ancestors originated earlier.

In this sense the proposition regarding the closeness of the poposaurid *Postosuchus* from the Upper Triassic deposits of India [15] to a tyrannosaurid ancestor is not quite correct. Its similarity with the tyrannosaurids in almost thirty places (some of which, in our view, have no phylogenetic value) need not obscure the essential differences between them. First, the paroccipital processes in *Postosuchus* skull join laterally not with the squamosals, but with the quadrates. In the carnosaurs, however, the squamosal forms a pocket for the proximal head of the quadrate. Second, the quasi-straight posture of *Postosuchus* was achieved by rotating the plane of the cotyloid cavity downward and slightly to the side, making contact with the femur from above. Third, even though *Postosuchus* is imaged on an original reconstruction in the manner of a digitigrade, the author can offer nothing that would support such a conclusion. Parrish [42] convincingly showed the inadequacy of this view and concluded that *Postosuchus* was plantigrade. These facts give no reason to prefer *Postosuchus* over other forms in the question of carnosaur origins.

## THE HISTORICAL DEVELOPMENT OF CARNOSAURS

In its fundamental features, the historical development of carnosaurs was governed by trends that were already distinguished at the very earliest stages and, perhaps, even in the carnosaur ancestors: predation and bipedalism. But these did not appear in equal measure in every line, and fundamental evolutionary trends realized in the group as a whole at the end of the Cretaceous can be traced in any of them. In spite of the fact that a number of features developed in parallel with coelurosaurs, the carnosaurs could not have mastered several of the narrow specializations as in the Cretaceous predators. Carnosaurs pretty much evolved in one direction with no drastic shifts into special adaptive zones. A similarly directed evolutionary process was in the main expressed externally as a progressive increase in body size.

Trends of a general nature that are intrinsic to all theropods can be seen together with specific trends that are found in carnosaurs. The universal nature of the first is linked with the perfection of bipedalism, which large body size limits (e. g., the distal region of the tibia is always large, but the articulation surface is less mature than in the small predators) and with predation, probably, transforming in some cases into feeding on carrion. No less significant a role was played by specific features that marked the departure of carnosaurs from the line of small bipedal predators: enlargement of the skull and simultaneous shortening of the neck and body, development of specialized teeth from large fang-like teeth, gradual reduction of the forelimbs to half their original size and shorter hind limbs or presacral vertebral region. Carnosaur skeletons exhibit fairly insignificant conversions. Narrowing of the frontal and temporal bones led to “merging” of the superior temporal fenestrae and the increase in head size led to abbreviation of the cervical vertebrae and the development of articulations between them. They had a ridge for attaching the pterygoid muscle. The ischia became smaller, whereas the pubes grew and a powerful distal “boot” developed. The hind limbs became more massive, the fourth trochanter decreased insignificantly, and the tarsi became measurably longer. The ascending process of the astragalus became a third as long as the tibia and widened, the calcaneum became even smaller.

The historical development of carnosaurs falls into two stages that make a gradual transition into each other: the first stage was characterized by the development of the families

Megalosauridae and Allosauridae; the second stage, in which carnosaurian features reached their highest expression, in the Tyrannosauridae. The Megalosauridae, including the most general and oldest forms, are the base of the carnosaurian phylogenetic tree. The Allosauridae descended from them at the start of the Late Jurassic and the Tyrannosauridae at the start of the Late Cretaceous. As regards the other families, they descended from the same Megalosauridae somewhat earlier (fig. 1), although the possibility that the aberrant Torvosauridae originated independently cannot be dismissed entirely.

Figure 1. Cladogram of the phylogenetic relationships among carnosaur families.

## MEGALOSAURIDAE

The famous *Megalosaurus bucklandi* Meyer from the Bathonian deposits of England that gave name to the most numerous and widespread family, is known only from isolated and unassociated bones. If all the remains that have been described do in fact belong to *Megalosaurus*, it displays a mosaic of characteristic features, some of which are intrinsic to the Allosauridae, others of which are intrinsic to the Tyrannosauridae, and some, such as for example the short, wide scapula, are probably intrinsic to Plesiomorphia. A similar collection of features creates several difficulties for classifying carnosaur, especially those established from fragmentary material. A tendency to preserve corresponding groups of features is not typical of the youngest genera (*Megalosaurus*, *Gasosaurus*, *Yangchuanosaurus*) indicates their high degree of variability, which is quite feasible for members of the most generalized family.

European Megalosauridae from the Middle and Upper Jurassic are represented by very incomplete specimens. *Megalosaurus nethercombensis* Huene was established from toothed jawbones and other postcranial bones [30]. Interestingly, the tibia is similar to that of *Magnosaurus andrewsi* Huene [31] in that it lacks the characteristic compression in the distal end in the front to rear direction.

Judging by the dentary bone, *Megalosaurus hesperis* Waldman [57] from the Bajocian deposits is obviously extremely similar to the more recent *M. bucklandi*. The premaxilla is very low and the anterior edge is sloped to the rear, which distinguishes it from other Megalosauridae.

To all appearances the genus *Megalosaurus* is the most generalized form in the family. If, however, there were in fact only 12 teeth on the upper jaw, then *Megalosaurus* may be a special form only slightly suited to be an ancestor of the “toothier” Allosauridae and Tyrannosauridae.

*Iliosuchus incognitus* Galton [32] was established from an isolated ilium characterized by a very mature central vertical ridge on its lateral side. A somewhat similar ridge was observed in *Stokesosaurus clevelandi* Romer [40] and very slight ridge was noted in *M. bucklandi*. *Iliosuchus* was probably close to both forms, but to a different degree.

Other European Megalosauridae are characterized by unusually tall vertebral neural processes. The Upper Jurassic *Metriacanthosaurus parkeri* Huene [30] is the most ancient of these. Its neural process are three times as tall as the body, whereas in other genera of all families, excluding Spinosauridae, the corresponding index is barely two. By this feature *Metriacanthosaurus* is similar to the more recent *Altispinax* or the allosaurid *Acrocanthosaurus*, although there are no other features that would unite them.

The better known Megalosauridae are from China. The Middle Jurassic *Gasosaurus constructus* Dong, Tang was established from a substantial skeletal region [22]. The humeri are

very broad in the proximal region and the ischia are very short in the front to rear direction, which is somewhat reminiscent of the prosauropod relations. The shape of the proximal region of the femora is unique: the head is withdrawn further in the medial direction than in other carnosaurs and separated from the high lesser trochanter by the low greater trochanter.

A more complete skeleton of *Yangchuanosaurus shangyouensis* Dong, Zhou, Zhang was found in the Upper Jurassic deposits of Szechuan province [23]. From these the remains of another species—*Y. magnus* Don, Zhou, Zhang—were established. These species display a unique combination of features, some of which are ceratosaurian (nasal ridge, supracotyloid ridge, narrow pubes) and some testify to close similarity to the Allosauridae, although there are no features that indicate direct kinship. *Y. shangyouensis*—the most ancient carnosaur whose skull was discovered—displays plesiomorphically high, but almost vertical quadrates, a dual horny ridge on the nasal bones. The upper cotyloid cavities merge above the temporal bones, which manifests itself in the allosaurid line immediately prior to the appearance of the Tyrannosauridae.

Along with *Gasosaurus*, the remains of the unique *Xuanhanosaurus qilixiaensis* Dong [21] were found in Middle Jurassic deposits. Metacarpal IV was preserved, and the same compression in the spinal vertebrae bodies as in the Allosauridae was noted.

The difficulties of exposing the relationships among the Megalosauridae are mostly due to the poor degree of material preservation and remain today. Megalosaurid remains from the Lower and Middle Jurassic deposits are distinguished by being the most highly fragmented (*Iliosuchus*, *Sarcosaurus*) and it is impossible to isolate among them the ancestor forms. Most genera come from the Upper Jurassic and therefore cannot be considered to be ancestors of the Allosauridae.

## TORVOSAURIDAE

The unique morphology of the Torvosauridae, of which we have already spoken, indicates that they branched off the base trunk of the carnosaurs very early or that they were extremely narrowly specialized. *Torvosaurus tanneri* from the Upper Jurassic of the USA [25] is characterized by a set of plesiomorphic features that are unknown in other forms despite their age. Limb elements are very massive, the first phalanx of the first manual digit is extremely short, whereas typically it is long in carnosaurs. According to these features *Torvosaurus* is descended from *Poekilopleuron* and *Erectopus* [30, 31], although they are more distinct in them. The most surprising feature, however, is the combination of dolichoiliac ilia with brachyiliac pubes and ischia. The torvosaurus have apomorphic features, although it is difficult to use these to compare *Torvosaurus* with other forms. The number of *Torvosaurus* teeth have been reduced to three in the premaxillary bones and ten in the upper jaw and dentary. The upper jaw bone is high and the dentary lacks a Meckelian sulcus [36].

*Poekilopleuron bucklandi* Eudes-Deslongchamps from the Bathonian deposits of France [30] was established from an incomplete forelimb, ribs, portions of a hind limb, and tail (the type has been lost). The caudal vertebrae show the earliest manifestation of extended prezygapophyses among carnosaurs. These prezygapophyses are more typical of the Cretaceous forms. The forelimbs are almost every bit as short and powerful as in *Torvosaurus*. The astragalus is moderately tall, the narrow ascending process has a small step on the posterior edge, with a low body. Judging by these features, *Poekilopleuron* has no genetic relationships with the Megalosauridae as was assumed [31] and must be included among the Torvosauridae. It is probably closer to *Erectopus*.

The genus *Erectopus* was established [31] from material that was initially described as *Megalosaurus superbus* Sauvage [46]. The basis for this was the teeth, even though postcranial material was known. This postcranial material was used to establish the species *E. sauvagei* Huene. It was assumed to have a pentadactyl hand, which raised certain doubts because of the incompleteness of the bones. The first phalanx of the first manual digit is short and massive. The lateral condyle of the femur is no larger than the medial. Its proximal end is distinct from that of any other known carnosaurs: the neck is inclined to the rear in such a manner that the head is located behind the trunk of the bone. The fourth trochanter is very offset in the proximal direction. The caudal vertebrae are long.

The unique morphology of the Torvosauridae indicates that they may be an advanced derivative of the prosauropods, although the long metatarsals and extended prezygapophyses contradict this. In any event, the structure of the forelimbs and pelvis compel us to think of them as being a specialized branch of carnosaurs. The lack of material, mainly skull material, precludes making more definitive statements regarding Torvosauridae origins.

## SPINOSAURIDAE

Perhaps the largest carnosaurs having a long snout region in the skull are found in the Cenomanian deposits of Egypt. *Spinosaurus aegyptiacus* Stromer is represented by fragmentary material [48]. The long spinal vertebrae have unusually tall neural processes that widen immediately above the arch then narrow and again widen distally. It is unlikely that all the spinal vertebrae are opisthocoelous. The lower jaw is low with a characteristically long symphyseal end. The lamellar bone has an opening like the Tyrannosauridae. The Early Cretaceous *Altispinax* [17] is undoubtedly a special form, even though it was established from only three connected spinal vertebrae. The length of the neural processes is more than four times the height of the body. These vertebrae are sometimes assigned to the genera *Metriacanthosaurus* or *Spinosaurus*, but this is apparently not quite correct because the neural processes of *Altispinax* are compressed immediately above the neural arch and do not widen as in the aforementioned genera.

It is rather difficult to make judgments about the genetic links of the Spinosauridae because their features have “extended” to different groups. The opisthocoelous nature of the spinal vertebrae suggests a kinship with the Streptospondylidae, the opening on the lamellar bone—with the Tyrannosauridae, and the length of the neural processes—with some Megalosauridae. They are most likely close to the megalosaurid-tyrannosaurid line, although a similar mix of features and the shape of the neural and symphyseal end of the lower jaw characterize a family that was narrowly specialized and had mastered another adaptive zone, the roots of which must be sought at the beginning of the historical development of the carnosaurs.

Fragments of the lower jaw belonging to a carnivore having a “spinosaurian” type of symphyseal end were found in the Lower Cretaceous (Aptian) of Niger.

## ABELISAURIDAE

This unique family from the Cretaceous deposits of Argentina is, in our view, an assemblage. The Maastrichtian *Abelisaurus comahuensis* Bonaparte et Novas [11] is similar to them in terms of the number of teeth in the jaw and premaxillary bone and the shapes of these

bones, the paroccipital processes, and the shape of the postorbital and other bones, although the author believes that this species is different from the Tyrannosauridae. In any event, the closeness of *Abelisaurus* to other species in the allosaurid-tyrannosaurid line is extremely likely. The earlier *Carnotaurus* and *Xenotarsosaurus* [9] stand apart. They are distinguished not only by the shape of their skull and postcranial skeleton, but by structural details (tall, narrow jaw bones; preorbital “horns”; sharp division of the orbits; tall quadrates; small ascending process of the astragalus, et al.). It is quite possible that the lines that led to these two species came from the Megalosauridae quite long ago.

## STREPTOSPONDYLIDAE

These are distinguished among the European forms by a very long, narrow skull with long frontals; prefrontals skewed forward; long spinal vertebra bodies that are highly opisthocoelous relative to the Megalosauridae and Allosauridae; and by the wide pleurocoel. The apomorphic states of the cervical and spinal vertebrae along with the overall plesiomorphic state of the other skeletal features (wide frontals completely lacking a “block”, the low ascending process of the astragalus, and greater trochanter located on the same level as the femur head) suggest that the Streptospondylidae cannot be related to the allosaurid-tyrannosaurid line.

The Upper Jurassic *Eustreptospondylus oxoniensis* Walker [50], along with *Streptospondylus altdorfensis* Walker and *S. cuvieri* Owen and *S. major* Walker provide the most complete material. These form a group of carnosaurs that have a distinctly opisthocoelous presacral vertebra with pleurocoels.

*Piveteausaurus divesensis* Taquet, Walker was established from a braincase from the Callovian of France [44], which differs from that of *Allosaurus* [51]. A similarity was noted in the neurocranium of *Eustreptospondylus*, suggesting that *Piveteausaurus* is a member of the Streptospondylidae. This, however, remains to be confirmed.

## ALLOSAURIDAE

The second most numerous family consists of forms that are barely interlinked by direct genetic relationships. The most ancient (and probably ancestral) form is *Piatnitzkysaurus floresi* Bonaparte from the Lower Callovian of Argentina [10]. It is distinct from the other large Allosauridae in the following plesiomorphies: short ilium, very short pubic boot that is almost indistinguishable from the symphysis of the ischia, and long humeri. It is similar to the later carnosaurs in the arrangement of the superior temporal fenestrae; the presence of a pleurocoel in the cervical and anterior spinal vertebrae; the long, narrow scapula; the head of the femur, which exceeds the greater trochanter, and; the distinct lesser trochanter. These features are preserved or are more highly developed in the Allosauridae and Tyrannosauridae.

A more advanced form is *Szechuanosaurus campi* Dong, Zhou, Zhang [23] from the Upper Jurassic of China. It is similar to *Allosaurus* in several respects: the cervical vertebrae are opisthocoelous; the spinal vertebra are short; the posteroventral coracoid process is mature; and the lesser trochanter protrudes forward. The more primitive pelvic structure is manifested in a less mature pubic boot. Elements of the extremities are long and thinner than in other Allosauridae.



Besides those enumerated, other features that were merely noted in previous genera are mature in *Allosaurus fragilis* Marsh from the Upper Jurassic of the USA [40,41]: large maxillary sinuses, reduced ischial process on the ilium, large pubic boot, and a rectangular obturator process. On the whole, *Allosaurus* in its more concentrated form has many family features that connect it with the Tyrannosauridae. These are short, vertical quadrate bones; the shape of the contact between the temporals and upper occipital; the development of the surangular foramen; low neural processes; development of chevrons on the posterior caudal vertebrae; reduction of the ischial process on the ilium; powerful pubic boot, etc. Nevertheless, such features as five premaxillary teeth and the downward slope of the paroccipital processes suggest that *Allosaurus* could not have been the base of the tyrannosaurid trunk. This is, however, insufficient grounds to rule out the possibility of direct genetic kinship between the Allosauridae and Tyrannosauridae [15]. According to this view, these families are parallel lines because a rudimentary condyle of the talocrural joint is on the calcaneum in Allosauridae, but on the astragalus in Tyrannosauridae [15]. We believe that the appearance of a similar view is due to an incorrect homologization of the respective tubercles and recesses on the tarsals. We have seen no major differences in the structure of the talocrural articulation between *Allosaurus* and *Tarbosaurus*. An almost identical protuberance had developed on the calcaneum of *Tarbosaurus* as is found in *Allosaurus*, but smaller and slightly different in shape. Apparently it is even smoother in the *Tyrannosaurus* that Chatterjee [15] used for comparison. *Tarbosaurus* and *Tyrannosaurus* are so similar in every respect that it seems unlikely there would be any difference in the structure of their talocrural articulations. For this reason, there are almost no doubts regarding genetic links between Allosauridae and Tyrannosauridae.

*Marshosaurus bicentesimus* Madsen from the Upper Jurassic of the USA [40] was established from pelvic bones. Despite their small size, the shape of the ischia and proximal region of the pubes put it closer to *Allosaurus* than to *Piatnitzkysaurus* or *Szechuanosaurus*.

Very compressed spinal vertebrae that are typical of *Allosaurus* are seen in material from the Upper Cretaceous Lameta formation of India. They have been assigned to two species—*Ornithomimoides barasimlensis* Huene and *O. mobilis* Huene [32]. From these the odontoid of *Compsosuchus solus* Huene was identified, which displayed *Allosaurus* features that are absent in other taxa: cylindrical intercentrum; very compact pleurocentrum; and a transversely widened odontoid process. These features are more satisfactory proof of the similarity with *Allosaurus* than is the similarity of the spinal vertebrae, although the lack of comparable *Compsosuchus* and *Ornithomimoides* material allows the possibility that there were not three, but only one species of Allosauridae during the Late Cretaceous of India.

*Acrocanthosaurus atokensis* Stovall et Langston from the Albian stage of Oklahoma occupies an intermediate position between the Allosauridae and Tyrannosauridae. In addition to allosaurid features, it has, like the Tyrannosauridae, a zygomatic process, a wide postorbital edge, and mature pleurocoels on the posterior spinal vertebrae.

Genetic links between the designated families are illustrated by carnosaurs from the Cenomanian of Egypt—*Bahariasaurus ingens* Stromer [49] and *Carcharodontosaurus saharicus* Depéret, Savornin [19]—with which a similarity to the Tyrannosauridae is suggested [38]. The Egyptian Allosauridae are united with the latter by the following features: superior temporal fenestrae merge above the temporals, amphicoelous anterior spinal vertebrae, centrally located neural processes in the caudal vertebrae, drastic widening of the acromial region of the scapula, and triangular obturator process. There are features that unite the Egyptian forms with Allosauridae, but not with other carnosaurs. The wide but curved teeth as in *Szechuanosaurus* suggest that the

Egyptian forms found their way here from Laurasia at an evolutionary stage between *Acrocanthosaurus* and the Tyrannosauridae.

The tooth of *Diplotomodon horrificus* Leidy [39] from the Upper Cretaceous of New Jersey is similar to the teeth of *Carcharodontosaurus* and may be a later descendant of the Allosauridae.

*Shanshanosaurus huoyanshanensis* Dong from the Upper Cretaceous of China is similar to the Tyrannosauridae [20]. This is indicated by the large splenial aperture; short, high premaxilla; pleurocoels on the posterior spinal vertebrae; premaxillary teeth in the shape of incisors; and the mature pubic boot.

*Itemirus medullaris* Kurzanov [27] from the Turonian of Kazakhstan is, judging by the dorsal region of its braincase and the acute forward slope of its pterygoid processes, extremely similar to the Allosauridae and Tyrannosauridae.

Placing *Chilantaisaurus maortuensis* Hu [29] (from the Cenomanian of China) among the Megalosauridae raises certain questions. Visibly it is related to the Allosauridae with which it is similar in terms of the shape of the paroccipital processes, the short atlas, and medial displacement of the fibular condyle. Short quadrates and posterior tapering in the proximal region of the third basidigital support the placement of *Chilantaisaurus* in this family.

## TYRANNOSAURIDAE

This family is a more or less unique Upper Cretaceous group. *Albertosaurus*, *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* are extremely close genera. The Asiatic forms—*Alectrosaurus olseni* Gilmore [27] and *Alioramus remotus* Kurzanov [1] stand apart. They are more graceful, having a long skull, proportionally long elements of the hind limbs, and a large number of teeth. At the same time, *Alectrosaurus* and *Alioramus* have the distinct diagnostic properties of the Tyrannosauridae: merging superior temporal fenestrae and proximally tapering third basidigital.

The evolution of carnosaur form *Piatnitzkysaurus* to the Tyrannosauridae is seen in the increasing body size, transformation of the distal symphysis of the pubes into a “boot” and of the ischia into bacillary structures, and proximal tapering of the third basidigitals. In the skull the adductor fossa increased in size, the superior temporal fenestrae grew to the point of merging above the temporals, the maxillary and occipital sinuses developed, the quadrates grew smaller, and the number of teeth decreased. Two structures are not listed in this scheme of gradual transformations, either remaining plesiomorphic or the result of altering the evolutionary process. First, these paroccipital processes were not sloped downward as in the Allosauridae, but were oriented horizontally. Second, the cervical and anterior spinal vertebrae are amphicoelous or amphiplatycoelous, rather than opisthocoelous as in the Allosauridae.

Among the Tyrannosauridae, *Alectrosaurus* is perhaps the most generalized form and may be considered an ancestor of at least the Asiatic *Alioramus* and *Tarbosaurus*, although the first retains some plesiomorphic features—a long, low skull and large number of teeth. *Tarbosaurus*, however, is extremely similar to the North American *Tyrannosaurus* and is sometimes included in this genus as a unique species [3]. *Tyrannosaurus*, the North American *Daspletosaurus*, and *Albertosaurus* form a number of genera that are extremely similar in age and morphology and probably descended from a common ancestor—a role that *Albertosaurus* is suited for. The high degree of similarity between the American and Asiatic forms at the end of the Late Cretaceous leads us to assume a common ancestor and the possibility that the Tyrannosauridae migrated from

Asia into America or vice versa. Yet it is still unlikely that *Alectrosaurus* could have been an ancestral form with several advanced features in the structure of its extremities. Earlier forms must probably pretend to this role.

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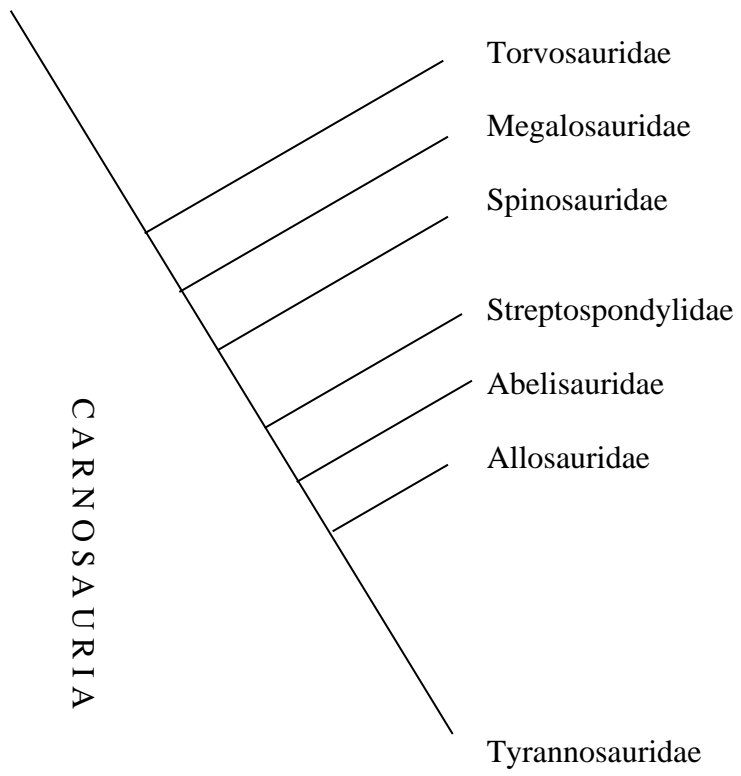


Figure 1. Cladogram of the phylogenetic relationships among carnosaur families.